

**REGULATION IMPACT ON SUBMERGED MACROPHYTE COMMUNITIES IN SOME
NORWEGIAN LAKES (1)**

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TO LIV, ERLEND, AND GRO

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The dissertation comprises the following five papers :

- I Rørslett, B., Green, N.W., Kvalvågnes, K. 1978: Underwater stereophotography as a tool in aquatic biology.
Aquat.Bot. 4: 73-81.
- II Rørslett, B. 1984a: Environmental factors and aquatic macrophyte response in regulated lakes - a statistical approach.
Aquat.Bot. 19: 199-220.
- III Rørslett, B. 1984b: Statistics of the underwater light field.
(manuscript)
- IV Rørslett, B. 1985a: Death of submerged macrophytes - actual field observations and some implications.
Aquat.Bot. (in press)
- V Rørslett, B. 1985b: Regulation impact on submerged macrophytes in the oligotrophic lakes of Setesdal, South Norway.
Verh.Int.Verein.Limnol. 22 (in press)

These papers are referred to by their Roman numerals (I-V) in the text.

The dissertation papers (I-V) are presented in a separate appendix.



1 INTRODUCTION

The aims of the present study can be summarized as follows :

- A) Develop sampling methods suitable for quantitative studies on submerged aquatic communities.
- B) Establish a theoretical framework to assess lake regulation impact on niche size and spatial position by statistical methods.
- C) Relate the response of the macrophytes to regulation-induced niche changes.

Some sixty percent of Norway's hydro-electric power potential has been developed so far (STATISTISK SENTRALBYRÅ 1983:12). On an area basis, lake regulations influence a major part of Scandinavian lakes. The regulation height of Norwegian reservoirs is commonly less than 10m. An estimated 23% is regulated less than 5m and some 22% is regulated 5-9.9m (STATISTISK SENTRALBYRÅ 1983:27).

There is a truly remarkable paucity of data on submerged macrophytes in regulated Scandinavian lakes. RØRSLETT (1980, V) summarized the scant data available. The true shore vegetation in regulated lakes is far better documented (WASSÉN 1966, NICKLASSON 1979, NILSSON 1981).

Based on qualitative field data only, BRAARUD (1928) reported negligible regulation impact on Isoëtes lacustris-dominated communities in the Norwegian lake Hurdalssjø (mean annual water-level range 3.6m, total range 5.3m). QUENNERSTEDT (1958) related changes in the vertical distribution of e.g. Isoëtes lacustris to the annual water-level range in North Swedish lakes and reservoirs. An interesting case was the lake Gardiken, then unregulated, but with a wide natural water-level fluctuation of some 4m annually (5.7m annual maximum). This lake harboured some Isoëtes lacustris, allegedly with reduced performance and restricted vertical extension. NILSSON (1981) investigated the dynamics of littoral species in the subsequently regulated Gardiken (a substantial 20m nominal regulation height), and found no traces of the former submerged communities. Submergents survived, however, in the upstream located lake Övra Björkvattnet with a 5.9m nominal regulation height.

According to QUENNERSTEDT (1958), increasing the extent of regulation would eventually decrease the vertical distribution of e.g. isoetid species. The isoetid communities are the prevailing benthic primary producers in the mainly oligotrophic Scandinavian lakes (LOHAMMAR 1965, BRETTUM 1971, SAND-JENSEN 1978). Thus, any changes in isoetid performance due to regulation impact might have negative ecological implications.

The regulation impact affects the niche space of the species inhabiting the lake floors, resulting in structural and dynamic changes in the vegetation (cf. Fig.1 below).

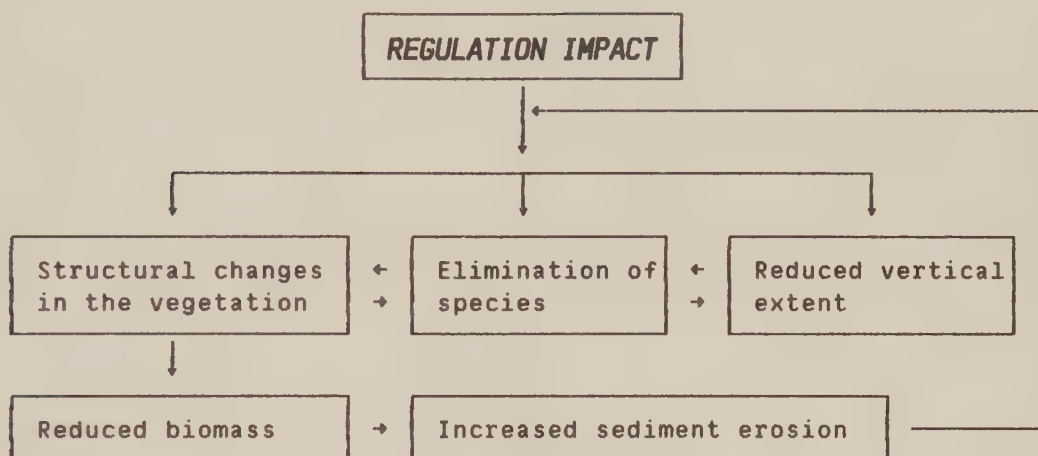


Fig. 1. The impact of a fluctuating water level invokes primarily the physical dimensions of the vegetation, niche space, adversely affecting the dynamics and performance of the submerged communities. Increased sediment erosion from a declining vegetation coverage initiates a positive feedback loop, thus enhancing the deterioration of macrophyte communities.

Quantitative assessment of regulation-induced impact on submerged macrophyte communities is impaired by the paucity and generally low spatial resolution of the currently available data. Hence, I initiated a research program directly addressing the spatial niche of the prevailing macrophytes in regulated, Norwegian lakes and reservoirs. The flow-chart for the response analysis in the niche space domain is outlined on Fig.2.

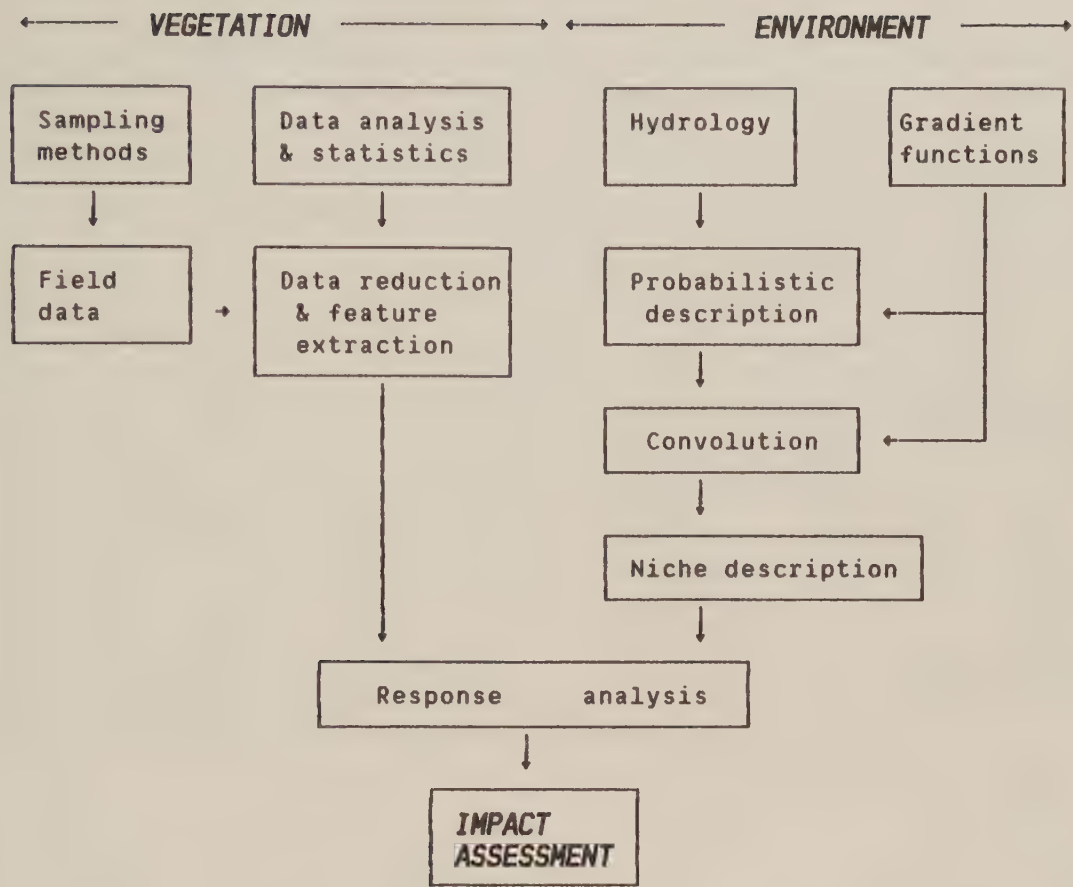


Fig. 2. Conceptual framework for quantitative assessment of regulation impact on submerged macrophyte communities. The response analysis is in the niche space domain.

The research program addresses the factors influencing the niche space of the submerged macrophytes. To this end, I deliberately focused on the spatial description of the submerged communities, more than on the species within the communities. The selected approach to community description also is highly unsophisticated; thus I consider the community as no more than the observed species array within a small area of the lake floor. Hence, the 'community' term carries no phytosociological implications whatsoever.

2 STUDIED LAKES AND THEIR VEGETATION

During the years 1976-1982, I collected a substantial data base on the vegetation, hydrology, morphometry, and hydrochemistry, of several Norwegian lakes. Partially, this data base arose from various contract works conducted by the Norwegian Institute for Water Research (NIVA, Oslo). Lake descriptions and preliminary results are mainly published in contract reports, hence it would be appropriate to shortly review the main features of these lakes and their vegetation here.

Initially, the data base encompassed 16 lakes. These lakes are listed in Tab. 1 and their geographical location is indicated on Fig. 3 below. These lakes span a wide range of areas, altitudes, and nominal extent of regulation. They are mainly clear-water, oligotrophic lakes. One mesotrophic lake, Steinsfjord, deviates from the other lakes, mainly due to a massive expansion of Elodea canadensis (RØRSLETT *et al.*, 1984). Data from subsets of the data base are used in the dissertation papers (II, III, IV, V). These subsets included only lakes with available hydrological data, and where the vegetation data were obtained by quantitative methods.

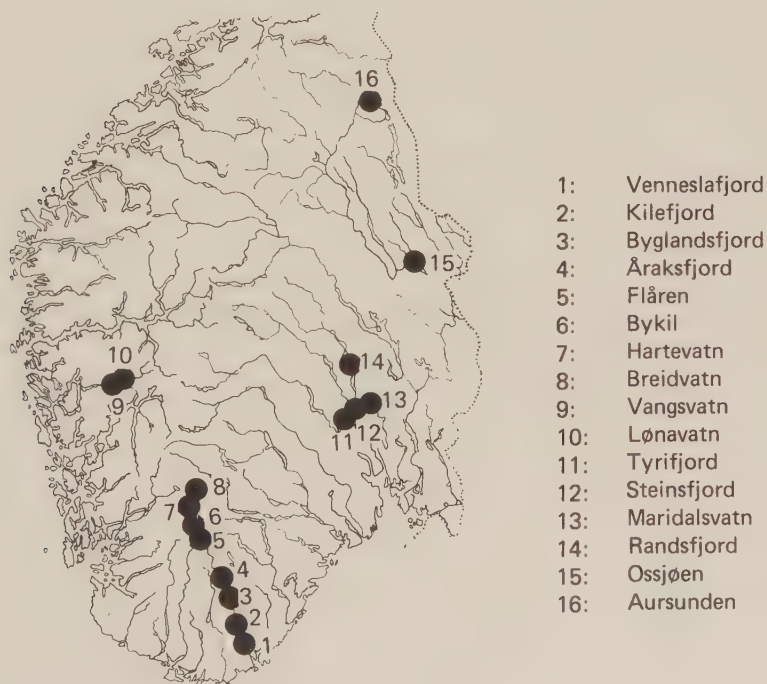


Fig. 3. Geographical location of the investigated lakes in Southern Norway.

Tab. 1. Investigated lakes. Morphometric and hydrological data.

Lake	Alti-	Area	Lake type [*]	Regulation height ^{**}	Water-level range		
	tude				Annual mean	max.	Total ^{***}
	(m)	(km ²)		(m)	(m)	(m)	(m)
Venneslafjord	38	1.7	UR	-	1.0		>1.0
Vangsvatn	46	8.0	UR	-	4.5	6.3	6.6
Tyrifjord	63	121.9	ST	1.0	2.0	2.9	3.5
Steinsfjord	63	13.9	ST	1.0	2.0	2.9	3.5
Lønavatn	77	3.0	UR	-	1.5		>2.0
Randsfjord	134	136.9	ST	3.0	2.9	3.9	4.2
Maridalsvatn	148	3.9	DW	2.0	1.1	1.3	1.6
Kilefjord	167	5.5	DR	1.5	2.0	2.9	3.2
Byglandsfjord	202	30.7	ST	5.0	3.6	4.9	5.9
Åraksfjord	203	11.2	ST	5.0	3.5	4.9	5.0
Flåren	274	1.4	WB	-	1.5		>1.5
Ossjø	435	45.2	ST	6.6	5.9	6.6	6.6
Bykil	500	1.0	DR	2.0	<1.0		<1.0
Aursunden	689	44.0	ST	5.9	5.5	6.1	6.1
Hartevatn	757	6.0	ST	7.0	6.4	7.3	7.8
Breidvatn	897	3.1	ST	2.5	3.0	3.5	3.5

^{*}) Reservoir/lake types:
 UR= nominally unregulated DR= damping reservoir
 ST= storage reservoir WB= weir basin
 DW= drinking water reservoir

^{**}) Nominal regulation height as licensed by Norwegian authorities

^{***}) Total within-lake range for all years 1945-1982

Tab. 2. Optical and hydrochemical data from the investigated lakes.

LAKE	k_{PAR} -1 m	Secchi depth m	pH	Conduct- ivity ₁ mS m	HCO ₃ meq -3 m	P mg -3 m	N mg -3 m
Venneslafjord	0.36	8-10	5.2-5.8	1.1-2.2	80	6	180
Vangsvatn	0.46	5-9	5.9-6.5	0.9-2.1		9	180
Lønavatn	-	5-9	5.9-6.5	0.9-1.7		6	170
Tyrifjord	0.53	5-10	7.0	3.2	180	7	400
Steinsfjord	0.58	2-7	8.4	9.0	610	11	250
Randsfjord	0.54	4-9	7.0	3.8		5	450
Maridalsvatn	0.46	5-8	6.8	2.8	85	5	410
Kilefjord	0.35	9-12	5.2-5.8	1.1-1.7	45	7	190
Byglandsfjord	0.34	9-21	5.8-6.0	1.0-1.2	40	2	130
Åraksfjord	0.32	9-23	5.8-6.1	1.0-1.1	40	<2	140
Flåren	0.60	>4	5.7-6.3	1.1-2.8	50	5	150
Ossjøen	0.80	3-7	6.3	1.9	90	7	280
Bykil	0.37	9-12	5.6-6.3	0.9-1.4	40	4	140
Aursunden	0.45	6-10	7.25	3.3	320	5	250
Hartevatn	0.46	7-13	6.0-6.4	0.9-1.3	70	4	120
Breidvatn	0.29	10-18	6.2-6.6	0.9-1.1	70	3	140

Comments: Compiled from data obtained by the Norwegian Institute for Water Research (NIVA) from 1976 to 1982. Data from central lake sites.

k_{PAR} Estimated by averaging over all observations and depths for each site, using best-fit models as advocated in (III). Lake Steinsfjord value dropped to 0.54 when data from 1983-84 were included.

Secchi: Observed range given
depth

Others: Observed range given for small data series,
otherwise median values.

The vegetation data were acquired along two different lines of approach.

The species present in a lake were assessed mainly by examination of drift material in near-shore areas, and floristic inventory of a 200m shore-line, at one to a maximum of twelve sites in each lake. A representative range of sites was selected, spanning from strongly exposed habitats to sheltered bays. Special attention was paid to the in- and outflow areas in larger lakes.

The quantitative distribution of vegetation in the vertical gradient was studied by means of underwater stereophotography (I). A quadrat size of 0.25m^2 was used throughout. At any site, photographic sampling was depth-stratified random, and the vertical sampling density exceeded the pre-assigned minimum of 20 samples m^{-1} within the vegetated zone, whenever possible. Often a far higher sampling density was employed, up to a maximum of ~ 100 samples m^{-1} .

The site locations were pre-assigned before field work commenced, by a table of random numbers used as site coordinates. Once a set of potential sites were drawn, a stratified subset of sites spanning the exposure gradient was selected. This scheme could be followed only for the larger lakes, however. Cost expenditure and the need for access by road prevented the realization of a truly stratified random sampling scheme for all lakes in the Setesdal valley.

The observed species are listed in Tab. 3. The helophytes in general have negligible occurrence, and are not given in the table. Major helophytes are Equisetum fluviatile, Carex rostrata (Otra lakes), while other Carex species, e.g. C. acuta, and C. aquatilis, prevail in the Southeastern lakes. Tall helophytes, e.g. Phragmites australis, are confined to lake Steinsfjord.

The isoetids total 13 species. Six major species are present in nearly all lakes, viz. Eleocharis acicularis, Isoetes echinospora, Isoetes lacustris, Juncus bulbosus, Ranunculus reptans, and Subularia aquatica.

The total number of species per lake ranged from 10 to 37, while the number of permanently submerged species in each lake ranged from 0 to 29 (Tab. 3).

Tab. 3. Aquatic species found in the investigated lakes.

'o' = not permanently submerged

'●' = also found below lowest water level

Species/lake no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<u>Isoetids</u>																
Alopecurus aequalis	-	o	o	o	o	o	o	-	-	o	-	o	-	o	-	-
Crassula aquatica	-	o	o	o	o	o	-	-	-	-	-	-	-	-	-	-
Elatine hydropiper	-	-	-	o	o	o	-	-	-	-	-	-	-	-	-	-
Eleocharis acicularis	●	●	●	●	●	●	●	●	o	o	●	o	o	o	o	●
Isoetes echinospora	●	●	●	●	●	●	●	●	●	●	●	o	o	o	o	●
Isoetes lacustris	●	●	●	●	●	●	●	●	●	●	●	-	●	●	-	●
Juncus bulbosus	●	●	●	o	o	o	●	●	●	●	●	o	●	o	o	o
Limosella aquatica	-	o	o	o	o	o	-	-	-	-	-	-	-	-	-	-
Littorella uniflora	●	●	●	●	●	●	●	●	-	-	-	-	-	-	-	-
Lobelia dortmanna	●	●	●	●	●	●	●	●	-	-	-	-	-	-	-	-
Peplis portula	-	-	-	●	o	o	-	-	-	-	-	-	-	-	-	-
Ranunculus reptans	●	●	●	●	o	●	●	o	o	o	o	o	●	o	o	o
Subularia aquatica	o	o	o	●	o	●	o	o	o	o	o	o	●	o	o	o
Species/lake no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<u>Elodeids</u>																
Callitriche autumnalis	-	-	-	●	●	●	-	-	-	-	-	-	-	-	-	-
Callitriche hamulata	●	●	●	●	-	●	●	●	o	o	●	o	●	?	-	o
Callitriche verna	o	o	o	o	o	o	o	o	o	o	o	o	●	o	o	o
Chara spp.	-	-	-	-	●	-	-	-	-	-	-	-	-	●	-	-
Elodea canadensis	-	-	-	●	●	●	-	-	-	-	-	-	-	-	-	-
Myriophyllum alternifl.	●	●	●	●	●	●	●	-	-	-	●	-	●	●	-	-
Myriophyllum verticill	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-
Najas flexilis	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-
Nitella confervacea	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-
Nitella opaca/flexilis	●	●	●	●	●	●	●	●	●	●	-	-	-	-	●	●
Potamogeton alpinus	-	-	-	●	●	●	-	-	-	-	-	-	-	-	-	-
Potamogeton berchtold.	-	-	●	-	●	-	-	-	-	-	-	-	-	-	-	-
Potamogeton crispus	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-
Potamogeton gramineus	-	-	-	●	●	●	-	-	-	-	-	-	-	-	-	-
Potamogeton obtusif.	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-
Potamogeton panormit.	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-
Potamogeton perfoliat.	-	-	-	●	●	●	-	-	-	-	-	-	-	-	-	-
Potamogeton x nitens	-	-	-	●	●	-	-	-	-	-	-	-	-	-	-	-
Ranunculus conferv.	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-
Ranunculus peltatus	-	●	●	●	●	●	-	-	-	-	-	-	-	●	-	-
Utricularia intermedia	●	-	●	●	-	-	-	●	-	-	-	-	-	-	-	-
Utricularia minor	●	-	-	●	●	●	●	●	●	●	●	-	-	-	-	●
Utricularia ochroleuca	●	-	-	●	-	●	-	●	●	●	●	-	-	-	-	-
Utricularia vulgaris	●	●	●	●	●	●	●	●	●	●	●	-	-	-	-	-
Species/lake no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16

Tab. 3. (continued)
Aquatic species found in the investigated lakes.
'o' = not permanently submerged
'●' = also found below lowest water level

Species/lake no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
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Nymphaeids

Nuphar lutea	-	-	-	●	-	●	●	-	-	-	-	-	-	-	-	-
Polygonum amphibium	-	-	-	●	●	●	-	-	-	-	-	-	-	-	-	-
Potamogeton natans	-	●	●	●	●	●	●	-	-	-	-	-	-	-	-	-
Sagittaria sagittif.	-	-	-	o	o	o	-	-	-	-	-	-	-	-	-	-
Sparganium angustif.	●	●	●	o	o	o	●	●	●	●	●	o	●	o	o	o
Sparganium hyperboreum	-	-	-	-	-	-	-	-	-	-	-	-	-	o	-	-
Sparganium minimum	-	-	-	-	-	o	o	-	-	-	-	-	-	o	-	-

Species/lake no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
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Lemnids

Lemna minor	-	-	-	●	●	-	-	-	-	-	-	-	-	-	-	-
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Others

Fontinalis spp.	-	●	●	-	-	-	-	-	-	-	-	-	-	-	-	●
Sphagnum spp.	●	●	●	-	-	-	-	●	●	●	●	o	●	-	●	●
Spongilla cf.lacustris	●	●	●	●	-	●	●	●	●	●	●	-	●	-	●	●

Species/lake no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Species no. total	19	22	24	37	37	33	20	18	15	16	15	10	12	15	10	14
" " submerged	17	17	19	29	26	23	16	15	10	10	12	0	10	4	3	8

Lake no.

- 1=Venneslafjord
- 5=Stensfjord
- 9=Byglandsfjord
- 13=Bykil
- 2=Vangsvatn
- 6=Randsfjord
- 10=Åraksfjord
- 14=Aursunden
- 3=Lønavatn
- 7=Maridalsvatn
- 11=Flåren
- 15=Hartevatn
- 4=Tyrifjord
- 8=Kilefjord
- 12=Ossjøen
- 16=Breidvatn

3 SUMMARIES OF DISSERTATION PAPERS

(I): Stereophotography as a tool in aquatic biology

Quantitative sampling of submerged macrophyte communities in general is time-consuming and inefficient. Photography, however, provides a means to acquire such data fairly rapid and larger sampling regions can be accessed within reasonable time.

The paper (I) describes the technical details of a SCUBA diver-operated stereophotographic system, based upon 35mm cameras. The system uses dual cameras to produce high-quality stereophotographic images of a 0.25m^2 quadrat.

Some unique advantages of photographic sampling should be pointed out:

- an instantaneous record of the sampled area and prime data is combined by the processed image.
- the data, as photographic images, may be conveniently stored, analysed and re-analysed when the need arises.
- the community spatial relationships are preserved, and can be reconstructed in optical methods for measurement purposes.

The paper demonstrated the general validity of the photographic sampling approach. We also showed that loss of information was negligible provided the species present did not form a closed canopy, which precisely would be the normal case of submerged macrophyte communities dominated by isoetids. In fact, we pointed out that the increased sampling area compared to ordinary grab samplers would enhance the detection probability of small-grown, delicate species.

(II): Environmental factors and aquatic macrophyte response in regulated lakes - a statistical approach

The major environmental gradient in any lake correlates with depth. Plants are distributed across this vertical gradient according to niche preferences. Neglecting within-lake gradients, the spatial niche projects on to segments of the vertical gradient. Thus the niche description simplifies to the spatial coordinates of the vertical dimension, and the associated point-time probability distribution of environmental factors.

In regulated lakes, it is necessary to distinguish between depth and relative elevation, i.e., spatial position in the vertical gradient. Depth is the height of water overlaying the plants at any time, thus the instantaneous value may be nil.

The basic idea underlying (II) is very simple:

Given the probability distribution of the water levels, all factors can be related to the spatial position in the vertical environmental gradient

The optimal depth and elevation datum is shown to be the median water level. The datum provides for translation of the probability distribution function (pdf) of the water levels, p_v , such that

Expected value of a gradient function

= Convolution of function by pdf p_v

It can be shown that this represents a mapping from a Lagrangian into a Eulerian coordinate system. The paper (II) considers only (weakly) stationary stochastic processes, and as such represents a first-order approximation to the statistics of environmental factors.

The selected approach leads to a number of interesting consequences. In the z -domain (Eulerian coordinates), the time-averaged Lagrangian (depth) functions are vertically displaced depending upon the pdf p_v . The impact of regulation is assessed by recomputing any gradient function convolution with a Dirac delta-function pdf.

Depth in its time-averaged sense is not equivalent to relative elevation when the water level fluctuates throughout time. The magnitude of the discrepancy is generally large in shallow waters, where many species attain peak performance. The bias occurring when depth is used in lieu of vertical position, can be evaluated analytically for known pdf's p_v . For a sinusoidal water level fluctuation, the bias peaks at the median water level. Lake data demonstrated significant bias over the entire vertical gradient.

Environmental stress factors, e.g., ice-scour, influence aquatics over a much larger part of the vertical gradient with a variable water level. The exact vertical distribution of the factor depends critically on the pdf p_v . Thus, lakes with closely similar ranges of water level fluctuations can show quite different vertical distributions. Factors operating through threshold statistics are most adversely influenced by a time-varying water level. Using a simplified statistical model, this is demonstrated for subsurface irradiance.

In general, regulation impact results in a compressed vertical niche. Simultaneously, the potential niche is shifted into deeper waters. Vegetation data from nine oligotrophic, regulated Norwegian lakes show significant correlation to the reduced vertical niche defined by ice-scour and threshold irradiance. Water-level schedules determine the actual vegetational response; thus, the total probability distribution of water levels should replace the regulation height or mean annual range of water level variation in an analysis of response features.

(III): Statistics of the underwater light field

Subsurface irradiance is a major environmental factor influencing the submerged macrophyte communities in freshwater lakes. The underwater light field is highly variable in space and time. The inherent variability of the light field renders the statistical analysis of potential macrophyte-light relations difficult. However, once a statistical description is established, hypotheses of macrophyte response to the light factor can be formulated and tested.

In a previous paper (II), the vertical attenuation coefficient was assumed to follow a Normal law. This paper (III) extends the statistical analysis. Based upon the Normality assumption, the light field can be shown to follow a Lognormal law at any depth. The expectation and variance have closed-form expressions for a stationary water level. The stochastic description enables the definition of derived functions, e.g., the expected duration and intensity of the underwater light field below any selected threshold value. The impact of a fluctuating water level can be assessed as well, using the convolution method outlined in (II). In this case, neither expected light intensity nor its variance can be expressed in closed form.

The Normality assumption is justified initially by the Central Limit Theorem, since the scattering and absorption of subsurface irradiance is caused by several partially independent factors. Using a large data base of light measurements from Norwegian lakes, the paper demonstrates this assumption to hold in general for field data. The studied lakes were mainly oligotrophic. The two productive lakes included did fit the Normality model, however.

(IV): Death of submerged macrophytes - actual field observations and some implications

This paper addresses macrophyte death incidents observed in the lakes Tyrifjord and Steinsfjord. The spatial distribution of rooted, dead macrophytes was obtained by photographic sampling.

Sudden death of a macrophyte differs from the normal seasonal growth-senescence pattern. Whenever the mortality rate exceeds the regeneration capacity, population performance and dynamics are adversely affected. Submerged macrophytes inhabit a hostile environment, and might easily succumb to prolonged periods of unfavorable environmental conditions. Two hypotheses are put forward in (IV):

- i) Environmental-induced mortality can regulate the spatial performance, i.e., the niche extent.
- ii) A species' susceptibility increases with the life-span length.

These hypothetical assertions were tested by various statistical methods.

Identifiable sudden death incidents occurred in less than 5% of the samples (N=3257). The major species in the submerged communities of each lake generally prevailed in these incidents.

Sufficient data points for the dominating isoetid Isoetes lacustris at two exposed Tyrifjord sites enabled a statistical analysis of death incidents within the vertical gradient. Mortality rate increased sharply towards the lower limit of the zone colonized by I. lacustris. This would be expected if the control factor had an exponential depth distribution. Using log-transformed mortality rates, neither depth nor expected light intensity proved efficient in modelling the observed spatial mortality distribution, however.

An alternative approach, based upon a theoretical dose-response model with an implicit critical threshold irradiance, resulted in a highly significant relation ($R^2=95.8\%$, $P<0.001$) between probit-transformed mortality and a hazard function derived from light threshold statistics.

(V): Regulation impact on submerged macrophytes in the oligotrophic lakes of Setesdal, South Norway

This paper reports the vegetational details of seven oligotrophic lakes in the Otra watercourse, Setesdal valley (South Norway). These lakes have closely similar hydrochemistry, and all are highly transparent with Secchi-disc readings from 10 to 23m. The nominal regulation heights are 2.0 to 7.0m.

Macrophyte communities were dominated by isoetid species; Isoëtes lacustris, I. echinospora, and Littorella uniflora. Helophytes had negligible occurrence in five of the seven lakes. The number of submerged species declined significantly with increasing lake altitude, and also with extent of regulation. When only permanently submerged species were included, the species richness correlated only to regulation extent.

Submerged macrophytes divided into shallow-, intermediate- and deep-water species. Community distribution, using time-averaged depths, in the vertical gradient correlated significantly to the extent of ice-scour and threshold irradiance probability. Increasing regulation heights successively eliminated the shallow- and intermediate-water species, thus, only a deep-water community of Nitella cf. flexilis, bryophytes (mainly Sphagnum subsecundum) and freshwater sponges (Spongilla cf. lacustris) survived in the most heavily regulated lake. Perennial isoetids, mainly Isoëtes lacustris, did occur to a water-level range exceeding 3.6m annual mean and 5.9m total, however.

4 CONCLUDING DISCUSSION

The present study demonstrated some important facts regarding the lakes impacted by man-made water-level schedules and their vegetation.

Firstly, the main environmental gradient of all lakes related to the vertical spatial gradient, confirming the assertion put forward in HUTCHINSON (1975:408 et seq.). Thus, niche description <1> simplifies to the evaluation of the potential factors within segments of this gradient.

The necessity of discerning vertical position of a submerged community from its occurrence depth became apparent, however. The vertical position can be measured directly in the field, whereas the depth associated with this point in space can only be derived from computations based upon statistics of the water-level fluctuations. This important distinction is stressed in (II). Put simply, this is the key to regulation impact assessment. With any depth-related environmental factor, its expectation at some position in the vertical gradient implies a mapping from a Lagrangian (or moving coordinate) system into an Eulerian, or fixed-coordinate system. This mapping is obtained as a convolution integral (II).

Secondly, the vertical distribution of the submerged communities in the studied lakes followed easily generalized patterns. This distribution is a doubly-exponential decline below the depth of peak abundance, thus indicating a common limiting factor for all species (RØRSLETT 1983, IV, V). Deep-water community patchiness induces heavy rippling of the vertical distribution curves. This is a major feature, obtainable by the enhanced spatial resolution provided for by the photographic sampling method (I).

<1> Unfortunately, the concepts of 'niche' and 'habitat' are ambiguous and confused in the literature (cf. WHITTAKER et al. 1973, CHRISTIANSEN & FENCHEL 1977, ALLEY 1982, AARSSSEN 1984). Partly, this ambiguity stems from a failure to recognize that any real (i.e., existing) niche implies a spatial (or habitat) aspect, thus, delineation of 'habitat' from 'niche' cannot apply spatial criteria only.

Thirdly, niche space description involved mainly the physical dimensions of the environment ambient to the submerged species. Thus, niche space for the dominant species Isoëtes lacustris could be defined by two separate factors, viz. ice-scour (upper spatial limit) and thresholding light intensity (lower spatial limit).

A fluctuating water level induces environmental stochasticity with any depth-related and depth-varying factor, as seen from the literally fixed point of view of a submerged community. Spectral analysis of the water-level time series demonstrated the significance of low-frequent fluctuation patterns (RØRSLETT 1983, V). All lakes analyzed by this method had dominant annual spectral peaks ($f=1 \text{ yr}^{-1}$). Frequencies up to $f=4 \text{ yr}^{-1}$ accounted for 80% or more of total variance of these time series. Thus, perennial species would be exposed to a clearly repeating annual pattern of water-level changes.

According to some recent ecological theories, e.g., CHRISTIANSEN & FENCHEL (1977), increased environmental stochasticity would lead to wider ecological niches for the impacted species. This hypothesis was not supported by my study. Spatial niche extent of the submerged species generally decreased in the strongly regulated lakes. Concomitantly, the niche was displaced towards deeper waters (II, V). Partly, this could be caused by a restricted niche space, due to environmental factors operating through thresholds. In (IV), the importance of thresholding light intensity was demonstrated for Isoëtes lacustris. A fluctuating water level would augment the probability of encountering critical thresholds at vertical positions corresponding to fringe habitats, thus, mortality rates would be expected to increase sharply in such areas (IV).

The species richness in the studied lakes <1> related to three factors, viz. altitude, lake area, and extent of regulation. Thus, a multiple linear regression had a coefficient of determination (R^2) 81.8% ($P<0.01$). Regression coefficients showed species richness to be positively related to lake area, and negatively related to altitude and extent of regulation. The regression equation was:

$$S = 20.53 - 1.96 \Delta W - 0.012 H + 0.075 A$$

<1> Excluding the meso-eutrophic lake Steinsfjord.

where S = number of submerged species

ΔW = mean annual range of water-level (m)

H = Lake altitude (m a.s.l.)

A = Lake area (km^2)

In all lakes, again with Steinsfjord as an exception, the submerged communities had one to three strongly prevailing species, regardless of the actual size of the lake species pool. Thus, species richness per se might not be that important parameter in a description of lake vegetation, when oligotrophic Scandinavian lakes are concerned. I consider this observation to justify the initial emphasis on a total community description. Furthermore, since the isoetid Isoetes lacustris proved to be the outstanding species in nearly all my lakes, regulation impact assessment might, to a first-order approximation, be based upon niche space analysis for solely that particular species.

The vertical niche displacement, due to regulation impact, can be estimated from the weighted mean spatial position, or characteristic depth D_c <1>, of the submerged communities. In the studied lakes, within-lake variation of the characteristic depth was insignificant (RØRSLETT 1983). The regression equation relating D_c to the regulation extent was:

$$\text{Log}_{10}(D_c) = 0.28 + 0.12 \Delta W$$

where ΔW = mean annual range of water-level (m)

Although highly statistically significant ($P < 0.001$), the demonstrated relationship between D_c and regulation extent clearly cannot be extrapolated outside the observed range of regulation heights. This relationship pertains to the total submerged community, and does not account for niche displacements of individual species. Actually, by mapping estimated niche boundaries of Isoetes lacustris onto the regression relationship, (II) demonstrated the niche extent of this species to be rather weakly related to the range of water-level fluctuations in the studied lakes. Its niche size would be predictable, however, were the probability distribution of the water-level schedule used rather than the mean fluctuation range.

<1> Depth applied in its time-averaged sense, i.e., the expected height of the water column overlaying the community (cf. II, V).

Furthermore, the general trend towards communities dominated by stone-worts and bryophytes in the strongly impacted lakes urgently needs positive corroboration. My data showed that such communities prevailed in Hartevatn, a lake nominally regulated 7.0m. As to the fate of these species in lakes regulated 10m or more, nothing is known. It should be pointed out, however, that such excessively regulated lakes could harbour weakly developed communities of annual isoetids and amphiphytes, e.g., from the genera Eleocharis, Ranunculus, Callitriche and Sparganium. Such communities have been reported from Norwegian lakes regulated 9-25m (RØRSLETT 1980, JOHANNESSEN et al. 1984). Their spatial extent and production is negligible compared to the unregulated lake, however.

Impact assessment initially was a major aim for this study. The changes in niche size for the submerged species would likely be an important indication of such impact. Based upon the niche boundary relations for Isoëtes lacustris reported in (II,IV,V), the niche displacement and compression for this species would be obtainable for any lake with given water-level schedule. An example of the niche size prediction would be the lakes Aursunden and Ossjøen. These lakes are nominally regulated 5.9 and 6.6m, respectively, and their draw-down patterns are closely similar. Spatial extent of the Isoëtes lacustris niche in Aursunden is estimated at 5 and 2m for the pre- and post-regulation situation, respectively. The corresponding estimates for the lake Ossjøen are 2.5 and 0m. Lake Aursunden indeed harbours a submerged community with thriving Isoëtes, while this species is completely lacking in Ossjøen.

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